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INVASION NOTE

Invasive species and climate change: *Conyza canadensis* (L.) Cronquist as a tool for assessing the invasibility of natural plant communities along an aridity gradient

Or-Leyl Har-Edom · Marcelo Sternberg

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Abstract The predicted reduction in precipitation in the eastern Mediterranean due to climate change may expose the natural plant communities to invasive species. We assessed whether natural plant communities along an aridity gradient in Israel were resistant to invasion by considering differences in abiotic conditions and community characteristics in these regions. We considered *Conyza canadensis* as a model plant as it is a common invader in the region. We examined the mechanisms and functional traits of both the plant communities and *C. canadensis* that promote or discourage invasion. Study sites represented a rainfall gradient with four ecosystem types: mesic Mediterranean, Mediterranean, semiarid and arid. Our results showed that the mechanisms of community invasion resistance varied along the aridity gradient. At the arid and semiarid sites, water deficiency impaired the establishment of *C. canadensis*. At the mesic Mediterranean site, plant competition had a negative effect on *C. canadensis* performance, thus greatly reducing the likelihood of its establishment. We conclude that a decrease in regional precipitation due to climate change may not affect intrinsic resistance characteristics of natural plant communities to invasion in the area.

O.-L. Har-Edom · M. Sternberg (✉)
Department of Plant Sciences, Faculty of Life Sciences, Tel Aviv University, Tel Aviv 69978, Israel
e-mail: MarceloS@tauex.tau.ac.il

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Introduction

Global climate change and invasive species are quickly becoming two of the most important problems in natural and human managed ecosystems (Mack and D'Antonio 1998). While invasiveness (the capacity to invade) is a property of the invasive species, invasibility is a property of the native community. Invasibility can be termed as the sensitivity of a community to invasion by non-native species. Our understanding of the processes which cause species to invade certain ecosystems, or what makes one community more invasible than others, is still limited (Emery and Gross 2006; Prieur-Richard and Lavorel 2000). One of the pioneering theories suggests that increased species richness in a community enhances its resistance to invasion (Elton 1958), however the experimental results corresponding to this theory are inconsistent (Prieur-Richard et al. 2002; Wardle et al. 2008).

As temperatures and precipitation regimes continue to change, so do the ranges suitable to exotic species (Bradley et al. 2009). An increase in temperature might shift Mediterranean climates poleward, allowing invasive species to spread into regions that were previously too cold, while at the same time disappearing from other regions (Potter et al. 2009). Similarly, increased water availability could reduce abiotic resistance and facilitate invasion, whereas drought may promote resistance (Thomsen et al. 2006). These predictions agree with current knowledge regarding the effects of changes in temperature, precipitation and soil moisture on the properties and, consequently, invasibility of ecosystems (Davis et al. 2000; Dukes and Mooney 1999).

Most invasive species in Israel are annuals that predominantly invade managed or disturbed areas, such as agricultural fields and roadsides (Dafni and Heller 1980, 1990). However, some invasive species have also been observed in natural areas, suggesting that this problem will intensify unless preventive measures are applied (Bar et al. 2004; Dufour-Dror 2005).

Changes in rainfall regimes are expected to cause shifts in plant community composition in proximal communities along climatic gradients. Therefore, rainfall gradients occurring over relatively short geographical distances, such as the north-south climatic gradient in Israel, provide an ideal framework for studying changes in composition and dynamics of plant communities in response to climate change (Petru et al. 2006).

In the present study, field experiments were carried out in four distinct ecosystems along the north-south rainfall gradient in Israel. The aims of the present study were: (1) to assess the resistance of natural plant communities to species invasion along an aridity gradient, as a function of changes in environmental conditions and community composition and structure; and (2) to assess the success of an invasive species as a function of rainfall conditions and competition intensity. In particular, we asked the following questions: (a) does invasibility increase when disturbance removes native vegetation? and, (b) does invasibility decrease with increasing aridity?

Methods

Study sites

The study was carried out at four experimental sites in Israel during the 2005/2006 growing season. The sites are situated along a 245-km-long climatic gradient running from the Galilee in the north to the Negev desert in the south. These sites represent, respectively, mesic Mediterranean (MM), Mediterranean (M), semi-arid (S), and arid (A) ecosystems (see Table 1). All sites lay on the same calcareous (hard limestone) bedrock and were positioned on south-facing slopes. The study sites were protected by a fence to exclude the domestic grazers such as cattle, sheep and goats. The climate for all sites is Mediterranean, with mild and rainy winters (October–April) and long, hot, dry summers. The vegetative growing season is closely associated to the temporal distribution of rainfall. Germination of annuals and growth of most perennials begins soon after the first rains. The length of the typical rainy season increases from the desert (December to March) to the Mediterranean (October to May). It is important to note that rainfall in the semiarid and arid sites was below average during the study period. Both sites received only about 60% of the long-term mean annual rainfall (Table 1). This trend was also observed in the years following the present study (2007–2009).

Study species

The native plant community present in open gaps between shrubs in each site comprised both annual and perennial herbaceous plants. We selected *Conyza canadensis* (L.) Cronquist as a model invasive plant species as it is a common invader with a wide distribution in Israel (Zohary 1989). *C. canadensis* is an annual composite that grows in Israel within a wide range of rainfall conditions (100 to 900 mm), primarily in disturbed sites such as roadsides, old fields and waste dumps. *C. canadensis* is a native of North America and was first observed in Israel in 1940 (Feinbrun-Dothan and Danin 1998). Most of its life cycle takes place in winter: the seedlings emerge in the autumn, then overwinter as rosettes, elongate in spring (April–June), and begin flowering in June–July (Thébaud and Abbott 1995).

Experimental design

In summer 2005, 30 quadrats measuring 10 × 10 cm were marked at each station. The quadrats were randomly spread in open herbaceous gaps between shrubs over an area of approximately 50 m^2. Seeds of *C. canadensis* were collected haphazardly from stands near the Mediterranean station and germinated in a greenhouse under continuous light at 24°C. The

Table 1 Physical and biotic characteristics of the study sites along the aridity gradient

Ecosystem type	Rainfall (mm)		Temperature (°C)			Elevation (a.s.l)	Soil type	Vegetation formation
	LT	'06	Min.	Mean	Max.			
Arid (N 30°52′ E 34°46′)	90	52	13.6	19.1	26.1	470 m	Desert Lithosol	Open vegetation dominated by small shrubs and semi-shrubs such as *Zygophyllum dumosum*, *Artemisia sieberi* and *Hammada scoparia* and sparsely growing desert annuals, geophytes and hemicryptophytes
Semiarid (N 31°23′ E 34°54′)	300	190	13.2	18.4	24.8	590 m	Light Brown Rendzina	Dwarf-shrubs of *Sarcopoterium spinosum* and *Coridothymus capitatus* associated with herbaceous (chiefly annual) plant species
Mediterranean (N 31°42′ E 35°3′)	540	554	12.8	17.7	23.6	620 m	Terra Rossa	Dwarf-shrubland dominated by *Sarcopoterium spinosum* and a high diversity of herbaceous (mostly annual) plant species
Mesic Mediterranean (N 33°0′ E 35°14′)	780	778	13.5	18.1	23.4	500 m	Montmorillonitic Terra Rossa	Closed oak maquis (*Quercus calliprinos*) and open garrigue formations dominated by shrubs (e.g., *Calicotome villosa, Sarcopoterium spinosum*, *Cistus* spp.) and associated herbaceous plants

Temperature refers to annual means (mean minimum, mean, and mean maximum). Rainfall data were obtained from long-term (31 years—LT) rainfall data, as well as that corresponding to the 2005–2006 rainfall season—'06 (Israel Meteorological Service). Table adapted from Fleischer and Sternberg (2006)

seedlings were then transplanted into the delineated quadrats at the study sites following the first rains at each site (germination period of the natural herbaceous communities differed among sites along the gradient). *C. canadensis* seedlings shared the same age as the germinated vegetation at the transplanted site. The height of the transplanted seedlings was approximately 2 cm. The quadrats were randomly divided into three "competition" treatments, with 10 replicates per treatment, as follows: (1) the native herbaceous plant community (control), (2) the native herbaceous plant community plus the invasive plant (representing a relatively high density of 100 invasive plants per m^2), and (3) the invasive plant only, where all native plants were manually removed soon after germination. The aim of these treatments was to examine the reciprocal effects of competition on both *C. canadensis* and the native plant community.

Sampling

The plant communities were harvested at the peak of the growing season in April 2006 before the seeds were dispersed. During our study, *C. canadensis* flowering began earlier than expected (April–May 2006), and flowering individuals were removed after the top inflorescences had opened in order to avoid seed dispersal and contamination of the surrounding area. *C. canadensis* individuals that did not reach maturity were removed after plant senescence.

Plant density and species richness were estimated twice during the study—1 month after germination (results not shown) and during the harvest period. The aboveground biomass was weighed after drying at 85°C for 48 h. Species richness was estimated per sampling unit (0.1 m^2). This measurement represents the species richness which the invasive plant encounters in its local neighborhood, and not the entire site. *C. canadensis* reproductive effort was evaluated as the number of capitula per plant.

Due to severe drought at the arid station, seedlings emerged very late in the season and none of the transplanted *C. canadensis* seedlings survived the transplantation. Therefore, results presented refer to the remaining three stations: mesic Mediterranean, Mediterranean, and semiarid.

Data analysis

A two-way analysis of variance (ANOVA) was used to determine statistical differences among study sites and competition treatments (which we refer to as neighborhood effect). The tested variables were the aboveground biomass, density and species richness of the local vegetation, and aboveground biomass and number of capitula per individual for *C. canadensis*. Orthogonal comparisons (contrasts) were conducted as post-hoc comparisons between pairs of individual means in order to determine the effect of competition in each station. Residuals of aboveground biomass, plant density and species richness lacked normality (Shapiro-Wilk *W*-test) and data were therefore ranked (ties averaged) and an ANOVA applied to the ranked data. The analyses were therefore non-parametric (see Conover and Iman 1981). All statistical analysis was conducted with the JMP IN 5.0.1 software (SAS Institute Inc.).

Results

Community level

Aboveground biomass

Both native and invaded (samples where *C. canadensis* was transplanted) plant communities showed a significant trend of increasing plant biomass with increasing rainfall (Table 2; Fig. 1a). Competition between the local vegetation and *C. canadensis* had a significant effect only at the semiarid site, where lower biomass was noted in quadrats where *C. canadensis* was present.

Plant density

Location along the rainfall gradient had a significant effect on plant density. The highest plant density was found at the mesic Mediterranean site (Table 2; Fig. 1b). No significant effects of competition between the native plant communities and *C. canadensis* were observed.

Species richness

Species richness increased with increasing rainfall along the aridity gradient (Table 2; Fig. 1c). The resident species composition varied between samples, thus obscuring possible effects of species identity on the invasive plant. The presence of *C. canadensis* had no clear effect on species richness in the invaded samples.

Table 2 Results of two-way ANOVA for (1) effects of location along the climatic gradient (site) and (2) competition with *C. canadensis* (neighborhood effect) on native plant community properties

Source	DF	SS	*F*	*P*
Aboveground biomass				
Site	2	103406.7	63.69	**<0.001**
Neighb. eff.	1	814.02	1	0.321
Site × Neighb. eff.	2	8306.43	5.12	**0.009**
Error	54	43840.5		
Density				
Site	2	49219.16	22.4	**<0.001**
Neighb. eff.	1	564.27	0.51	0.477
Site × Neighb. eff.	2	1526.56	0.69	0.504
Error	54	59320.7		
Species richness				
Site	2	63857.61	28.37	**<0.001**
Neighb. eff.	1	281.67	0.25	0.619
Site × Neighb. eff.	2	2899.81	1.29	0.284
Error	54	60766.6		

Significant ($P < 0.05$) variables are in bold

Performance of the invasive plant

Aboveground biomass

Biomass production of *C. canadensis* was significantly affected by environmental conditions along the gradient and by competition with the respective local plant communities (Table 3; Fig. 2a), and showed an increasing trend with increasing rainfall. The effect of competition on biomass production of *C. canadensis* was most evident at the mesic Mediterranean site where plant densities were highest.

Reproductive effort

The reproductive effort of *C. canadensis* decreased with increasing aridity (Table 3; Fig. 2b). The highest number of capitula was found at the mesic Mediterranean site, whereas no capitula were found at the semiarid site. Competition with the local communities showed no significant effect on the reproductive effort.

Discussion

The results showed that all four communities have a relatively high resistance to invasion. This finding is

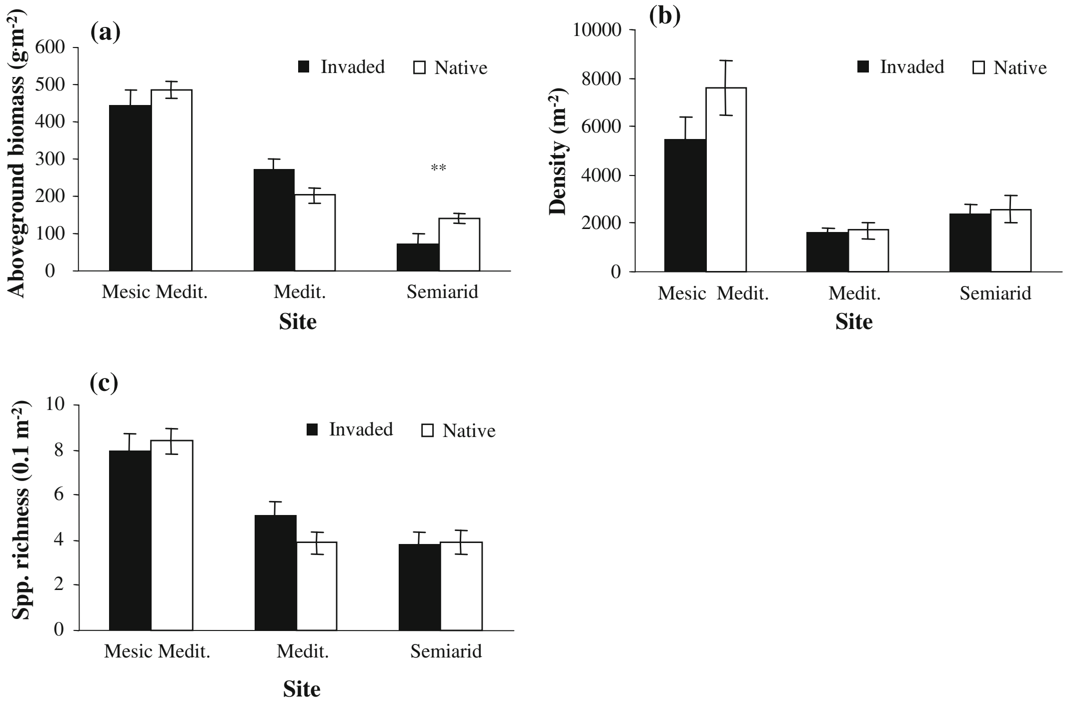

Fig. 1 Plant community aboveground biomass (**a**), density (**b**) and species richness (**c**) at three sites along the climatic gradient in Israel, mean values ± SE. Neighb. Eff. = neighborhood effect (competition with *C. canadensis*). Invaded = samples comprising the local community and a *C. canadensis* individual (biomass, density and species richness data do not include *C. canadensis*), Native = samples comprising only the local community. Medit. = Mediterranean. The statistical model is two-way ANOVA. Contrast analysis was conducted to determine the effect of competition between native and invaded samples at each site. Significance level: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$

Table 3 Results of two-way ANOVA for (1) effects of location along the climatic gradient (site) and (2) competition with the native plant community (neighborhood effect) on *C. canadensis* life traits

Source	DF	SS	*F*	Sig.
Aboveground biomass				
Site	2	5345.9	7.02	**0.002**
Neighb. eff.	1	3281.6	8.61	**0.005**
Site × Neighb. eff	2	374.66	0.49	0.615
Error	44	16762.14		
Capitula				
Site	2	2491.97	4.12	**0.023**
Neighb. eff.	1	447.76	1.48	0.23
Site × Neighb. eff.	2	326.86	0.54	0.587
Error	44	13312.03		

Significant ($P < 0.05$) variables are in bold

further supported by previous observations, which showed that eastern Mediterranean natural ecosystems are remarkably resistant to invasion, at least compared with other Mediterranean-type climatic regions (Dufour-Dror 2005; Groves 1991). Mechanisms of invasion resistance, however, seem to vary along the rainfall gradient. We believe that these mechanisms belong to one of two categories: (1) resistance that can be attributed to biotic interactions within the plant community, and (2) resistance that can be attributed to abiotic factors related to climate.

Community properties

Plant community aboveground biomass, density and species richness peaked at the mesic Mediterranean end of the gradient. These results are consistent with previously reported patterns of increasing biomass and species richness with increasing rainfall conditions in the region (Aronson and Shmida 1992; Kutiel et al. 2000). As all three community properties have been linked to competition intensity, it is likely that both inter- and intraspecific competition increased towards the higher rainfall end of the gradient

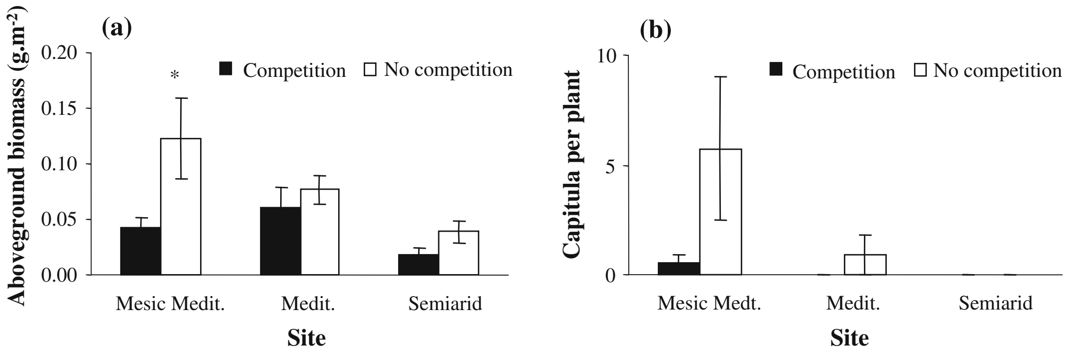

Fig. 2 *C. canadensis* aboveground biomass production (**a**) and reproductive effort evaluated as the number of capitula per plant (**b**) at three sites along the climatic gradient in Israel, mean values ± SE. Neighb. Eff. = neighborhood effect (competition with the local community). Competition = samples comprising a *C. canadensis* individual together with the local community, No competition = samples comprising only a *C. canadensis* individual. Medit. = Mediterranean. The statistical model is two-way ANOVA. Contrast analysis was conducted to determine the effect of competition between native and invaded samples at each site. Significance level: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$

(Fargione and Tilman 2005; Grime 1973; Naeem et al. 2000; Tilman 1988). The effect of increased competition on *C. canadensis* at the mesic Mediterranean site was clearly indicated by the decrease in aboveground biomass in quadrats with both *C. canadensis* and natural plant community, compared to the aboveground biomass in the controls from which the local plant community had been removed. These findings are supported by other studies that examined invasion resistance mechanisms, with *C. canadensis* as a model plant, and reported similar responses to competition with the local vegetation (Dimitrakopoulos et al. 2005; Thébaud et al. 1996). Interestingly, in contrast to the negative effects of the competition treatment on the invasive plant, the neighboring plants showed little response to the presence of *C. canadensis*. Significant negative effects of competition with the invasive plant were observed only on aboveground biomass production at the semiarid station, where community biomass was already quite low, i.e., when the local biomass was high, an addition of one more individual per sample, even when this individual was an invasive species, was not a significant factor.

Although increased competition at the wetter end of the rainfall gradient led to increased resistance to invasion, our present study does not elucidate which of the three community properties—aboveground biomass, plant density, or species richness—contributed the most to the ability of the plant community to resist invasion.

Climatic factors

The southern end of the climatic gradient in this study is characterized by lower rainfall than the northern end, shorter rainy season, and highly variable intervals between rainfall events. This results in an unpredictable environment, with high water-stress conditions that require plant species to possess adaptations for low water availability and prolonged droughts. In such environments, fast-growing, competitive species lose their advantage if they cannot survive between rainfall events (Petru et al. 2006; Sher et al. 2004). Therefore, it is interesting to examine whether increased aridity would result in increased invasion resistance regardless of competition. Our results support this idea, as aboveground biomass and reproductive effort of *C. canadensis* were significantly reduced as aridity increased. This was most notable at the arid site where *C. canadensis* seedlings did not survived their transplantation.

Conclusions and predictions

According to our results, all four plant communities were found to be highly resistant to invasion of *C. canadensis*, as both aboveground biomass and number of inflorescences of *C. canadensis* were low in all treatments with the majority not completing their life cycle. Interestingly, at the mesic Mediterranean site competition significantly affected invasion resistance while at the more arid sites resistance was affected by abiotic factors.

We suggest that a decrease in precipitation in the Mediterranean, semiarid and arid regions is not expected to reduce the invasion resistance of natural plant communities. Our results show that invasive species, as modeled by *C. canadensis*, are vulnerable to low water availability, despite its presence in a wide range of environmental conditions. Therefore a decrease in precipitation in these regions is likely to render them even more resistant to invasive herbaceous annuals that lack water-stress adaptations.

This study sheds new light on factors affecting plant community invasion resistance, since it was conducted in a natural setting as opposed to artificial assemblages commonly found in invasion studies. However, some additional factors should be taken into consideration when interpreting our results. Firstly, since shifts in plant community composition due to climate change may take long periods of time, the "space for time" approach was employed, i.e. extrapolation from spatial to temporal scale patterns. Moreover, this study presents only one year of experimental data and therefore should be repeated. Secondly, despite its wide distribution, *C. canadensis* is a relatively drought-sensitive species, therefore in order to generalize the results of this study it would be important to conduct additional experiments using additional invasive species as models.

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